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Official Journal of the Association for the Study of Animal Behaviour

Edited by

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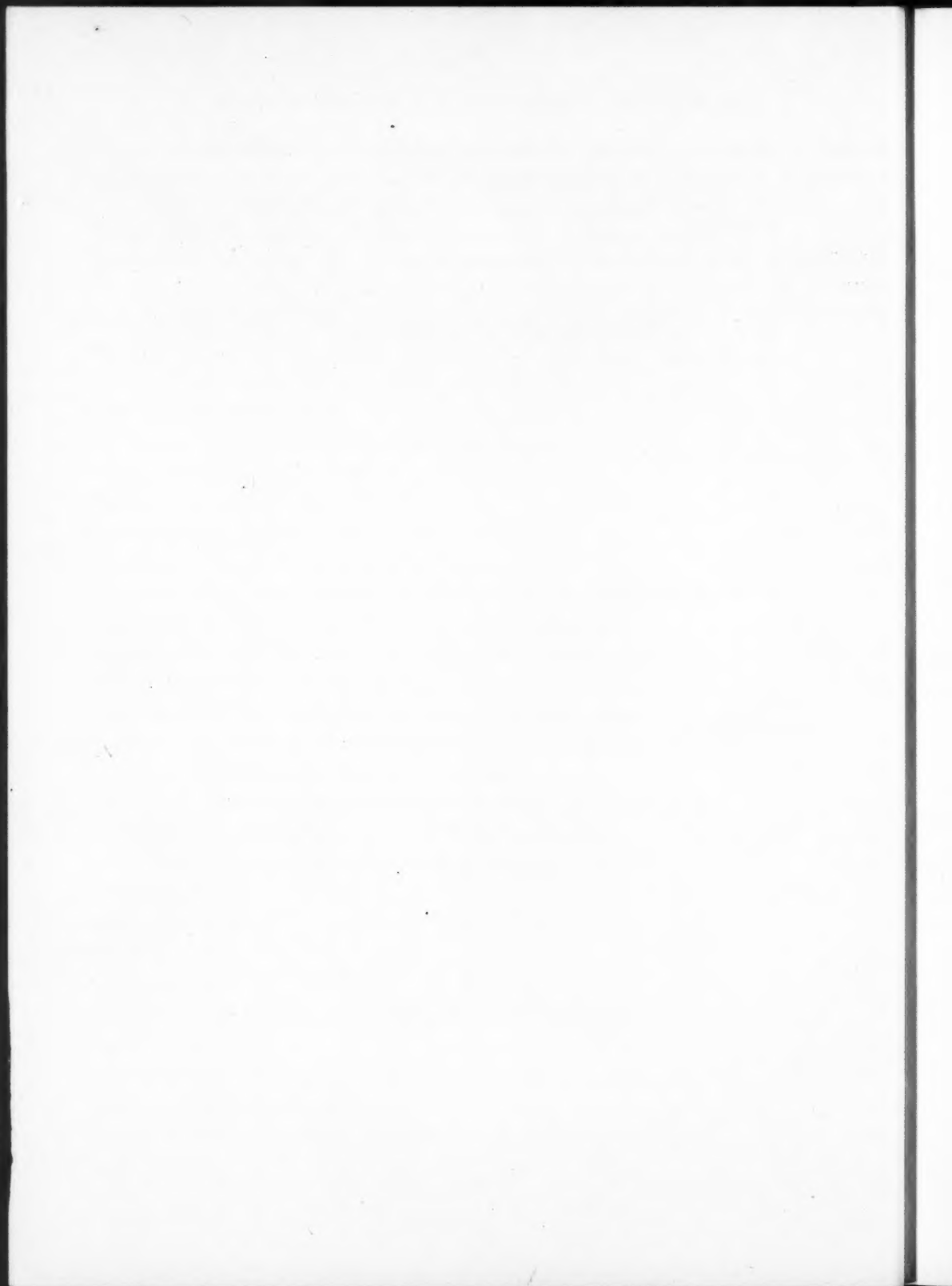
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Editorial

Contributed by DR. W. H. THORPE, M.A., Sc.D., F.R.S.

President of the Association for the Study of Animal Behaviour, 1949-1952.

THE study of animal behaviour, or comparative ethology as it is now very generally called, has undergone a great and rather surprising development in the course of the last twenty-five years. This development is certainly due to a number of circumstances, amongst them the steadily increasing interest in field natural history and ecology, but there is little doubt that the chief cause of this development was the publication by Lorenz in the years 1935-39 of the outlines of a theory of instinctive behaviour which, while owing much to earlier workers (*e.g.*, Wallace Craig), was new in some of its most important essentials and provided a new synthesis. But having said this we must not let it be thought that matters were at a standstill in England during this time. The pioneer work of Julian Huxley and F. B. Kirkman was the beginning of a new attitude and it was the enthusiasm of these two which led to the foundation in 1936 of the Institute (now Association) for the Study of Animal Behaviour. More recently, the publication of E. A. Armstrong's book "*Bird Display and Behaviour*," now translated into French, and the foundation of the journal "*Behaviour*" through the enthusiasm and initiative of N. Tinbergen were important events. No doubt the latter's recently published "*The Study of Instinct*" will be a further big stimulus to the analysis of innate behaviour.

Previous to Lorenz the idea of instinct, while accepted as an inescapable fact by field naturalists, was in general highly repugnant both to experimental zoologists and to psychologists. These had been so impressed by the conditioned reflex experiments and theories of Pavlov and other physiologists, and by the Associationist theories which sprang from the work of Thorndike and others in America, that they cherished the hope that all animal behaviour could be explained on the basis of simple reflex responses to simple stimuli and on the assumption that these could be built up by processes of association into the more complex behaviour which we observe every day. A contributory reason for this attitude was the absence of any comprehensive theory of instinct sufficiently precise to induce experimental work. Those who did write about and study the complex instincts tended to become merely descriptive, regarding the instinct as something given: a piece of behaviour into which it was useless, if not improper, to enquire further.

The coming, then, of a new theory had a two-fold effect, it stimulated immediately the experimental analysis of instinctive behaviour (as witness the admirable work of N. Tinbergen and his associates in Holland just prior to the war), and it assisted the realisation among experimental psychologists and others of the fact that there is much behaviour which cannot conceivably have been acquired in the individual life as a result of any kind of learning process. Consequently the present is a time of rapid advance in our subject and it is perhaps particularly in the study of the relations between instinct and learning that we are likely to see the most far-reaching developments in the near future. As Hebb* points out, in the past there has been among comparative psychologists a profound reluctance to postulate something going on within the animal which opens the door to one kind of stimulation and closes it to another. Now, however, the modern study of releasers and of drives is providing overwhelming evidence for just this phenomenon. At the same time there is taking place a highly significant development in neuro-physiology.

It was partly because so much of instinctive behaviour as observed by the naturalists seemed utterly impossible to account for neuro-physiologically that the psychologists tended to ignore it. At the same time they felt, not unnaturally, that a neuro-physiology which could account for so little of observed behaviour was hardly worth bothering about and so we got a school of psychologists who regarded the animal as a sort of magic box, into the construction of which it was impossible, or undesirable, to enquire; into which one put stimuli like pennies into a slot and out of which emerged behaviour in some way related, we knew not how, to the pennies which went in. Neuro-physiology still has a long way to go before it can give much precise guidance to the study of behaviour, but we should be very unrealistic and very blind if we failed to realise the stimulus which

* HEBB, D. O., 1951, The Role of Neurological Ideas in Psychology. *J. Personality*, 20, 39-55.

neuro-physiology can now offer to ethology. Hebb's recent theoretical discussion (*The Organisation of Behaviour*) is a most valuable guide and stimulus in this field.

As readers will know, the Association for the Study of Animal Behaviour has over many years produced a Bulletin at irregular intervals. For financial reasons this Bulletin had to be on a small scale and it was, moreover, launched at an exceedingly difficult time, very shortly before the beginning of the second World War. Nevertheless, we felt that it performed a function of some value, both as a journal open to papers dealing with almost any aspect of behaviourist study and as a vehicle for the publication of translations and summaries of certain foreign papers of outstanding importance to the science and not easy to come by in their original form. Besides this the Bulletin had made a practice of publishing a fair proportion of papers dealing with the behaviour of domestic animals.

The steadily increasing costs of paper and printing forced us to reconsider the whole future of the journal and we feel very gratified that as a result of a contract with Baillière, Tindall, & Cox, Ltd., the journal is to appear in future as a regular quarterly and is changing its name to the "*British Journal of Animal Behaviour*." We feel that this change should increase the scope and value of the journal enormously and we believe that it should be possible to transform it into an organ of wide and increasing importance to the science. We are, nevertheless, most anxious not to overlap to any appreciable extent with the other journals which deal with this subject, notably, the journal "*Behaviour*," which was founded with the good-will and co-operation of the Association; but we do in fact feel sure that any such overlap can be avoided and that, run on the right lines, each journal should profit from the existence of the other.

While it is not proposed to introduce any formal restriction of the type of paper which the new journal will publish, we anticipate that it will continue to show the main and what we feel to be the more desirable characteristics of the old. In particular, we think that the publication of reviews and summaries was a valuable service which should be continued and we are also impressed with the enormous field for applied behaviour studies.

Workers in animal husbandry, and veterinary science particularly, have opportunities not only to make advances of great practical utility in the development of the scientific basis on which their industries stand, but also, in so doing, to make important contributions to pure science itself. The distinction between pure and applied science is very largely an artificial one; in fact the difference comes down often to a matter of the length of view taken by the research worker, rather than the initial direction of his research. The worker in the applied field is often, in one respect at least, in an extremely favourable situation for prosecuting certain aspects of ethology in that he usually has a very large quantity of experimental material, material which it is often particularly easy to keep and maintain under controlled conditions and material which it is presumably easy to breed. Thus, while he may start his work in the hope of solving some practical problem in management and may indeed succeed in this aim, he may also produce results of great interest to the pure ethologist. A particularly promising field for co-operation of this kind undoubtedly concerns the changes in instinctive behaviour which take place with domestication. Here is a subject as yet scarcely touched upon, a subject for which the co-operation of the "pure" and the "applied" scientist is indispensable. Any behaviour worker dealing with domestic animals who does not take great pains to acquaint himself as fully as possible with what is known of the behaviour of the wild animals which have given rise to the domestic strains he studies may be missing a most valuable opportunity, if indeed he does not prevent the proper fruition of his work altogether. Similarly, there is great need for pure ethologists to concentrate, when conditions and opportunity offer, upon the behaviour of the wild animals from which domestic strains have been produced. It is hoped that the new journal will provide a steadily increasing stimulus to co-operation of this kind.

* * *

As this issue was about to go to press we learnt with regret of the sudden death of J. T. Edwards, D.Sc., M.R.C.V.S., whose work in the field of veterinary medicine and of animal behaviour is well known. An appreciation of his life and work will appear in a later issue.

The Inability of Honeybees to Communicate Colours

By C. R. RIBBANDS

Bee Research Department, Rothamsted Experimental Station

Introduction

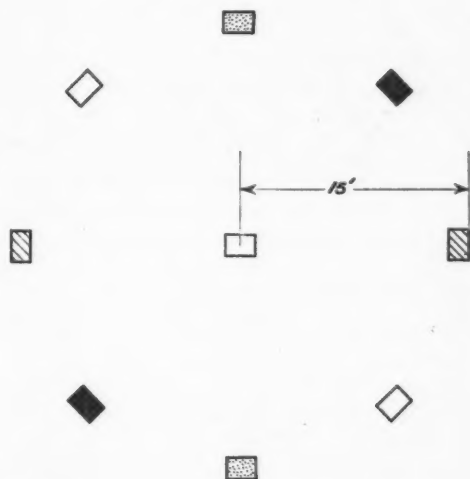
When dancing foragers stimulate their companions to search for a crop, the recruits perceive the scent which is adhering to the bodies of the dancers and search for that scent (v. Frisch 1923). In a control experiment v. Frisch fed a group of trained bees upon brilliantly coloured but scentless artificial flowers. He placed similar artefacts in the surrounding meadow, but the recruits did not attempt to visit them.

Françon (1939) claimed that foraging honeybees could communicate colour; his evidence was an uncontrolled observation.

Method

Pieces of white card, 8" x 5", were covered with either light blue, dark blue or yellow transparent filters (Diachrome) and also with a colourless transparent filter (Diachrome) which was said to absorb ultra-violet light. A similar set of cards were covered only with an opaque silver filter (Opachrome) which reflected ultra-violet light. In this way cards were obtained which reflected four different fairly pure colours. The filters were supplied by Dufay-Chromex, Ltd.

A card of one colour was placed on a lawn, and two cards of each of the four colours were spaced in a circle at a radius of 15 feet from the centre card (fig. 1). The cards in the circle occupied the same positions in all experiments. A group of honeybees having been trained to a watch-glass of sugar syrup on the centre card, one observer sat at the centre and killed off all additional recruits while another observer walked quickly round and round the circle of cards (supplied with empty watch-glasses) and killed and recorded the bees which had alighted on each card. Attempts to kill these bees were not always successful, so a record was kept of bees which were seen but not killed; the proportion of missed bees was small and these records were found to be immaterial. There were seldom more than one or two bees on a card at one time.



Results

Each experiment occupied a period of two hours, on either a morning or an afternoon; they were conducted on various dates between 8th March and 5th April, 1950. The results are displayed in Table 1. As the number of newcomers varied from experiment to experiment the results have been converted into percentages so that each trial becomes of equal value.

The number of new bees attracted to the cards at the circumferences was not related to the colour of the card to which the trained bees were flying. If honeybees were able to communicate the colour of the flowers which they had visited a different result would have been expected.

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- Françon, J. (1939). *The Mind of the Bee*. Transl. by H. Eltringham, London: Methuen.
Frisch, K. v. (1923). *Zool. Jb., Abt. 3*, 40: 1-186.

TABLE 1.

Percentages of honeybee recruits attracted to variously coloured cards.

Results are bracketed in heavy print when the bees went to cards of the training colour.

Colour in centre.	No. of bees killed at circumference.	Percentage of bees killed on each colour.			
		Dark Blue	Light Blue	Silver	Yellow
None	53	25	23	13	40
None	19	32	32	16	21
Yellow	27	11	52	0	(37)
Yellow	34	26	41	12	(21)
Dark Blue	10	(30)	60	0	10
Dark Blue	73	(25)	36	8	31
Light Blue	16	19	(42)	6	31
Light Blue	127	25	(31)	5	39
Silver	49	35	39	(6)	20
Silver	16	19	31	(6)	44
Mean percentage of bees killed on each colour		25	39	7	29
Mean percentage killed when centre and circumference colours were the same		27	36	6	29

The Term "Mimesis"

By R. A. HINDE

Ornithological Field Station, Madingley (Dept. Zoology, University of Cambridge)

With a reply by EDWARD A. ARMSTRONG

Cambridge.

In a recent paper Armstrong (1951) has discussed a number of types of animal behaviour which he groups together as "Mimesis." He defines mimesis as follows:—

"Mimesis occurs when, and implies that, the species is so constituted that the perception of certain innate behaviour-patterns performed by another animal is the releaser of the same, or closely similar innate behaviour-patterns by the observing individual."

In the course of his discussion Armstrong uses such terms as "Suggestibility," "Imitative susceptibility," and states that "Mimetic behaviour implies the tendency to respond to example. Immediately we form such a concept we pass from objectivistic ethology to psychology . . ." In brief, he treats his examples as though they had some property in common not shared by other examples of instinctive behaviour, and implies that they can only be discussed with the aid of certain rather vague terms. The present paper is limited to an attempt to stimulate further discussion by examining the extent to which the category of "Mimetic behaviour," as used by Armstrong, is a real one. Knowledge of Armstrong's paper is assumed.

For the purpose of the immediate discussion we may use Armstrong's definition of mimesis, but it should be noted that:—

(i) The term "releaser" is usually used in a rather different sense (Thorpe, 1951), and always refers to an external stimulus situation. The suggestion that the *perception* could be the releaser is terminologically incorrect.

(ii) The words ". . . is the releaser" imply that any other stimuli which influence the behaviour have, at most, a guiding influence. This seems rather improbable: when a bird is feeding in a flock its behaviour is released by the food as well as by the behaviour of its neighbours. The behaviour of the actor has at most a *releasing influence* on that of the reactor.

(iii) The words "Mimesis occurs when, and implies that, the species is so constituted . . ." imply that mimesis occurs whenever a species

has a potentiality to behave in a particular way, and not simply when it actually does so. These last two points are, of course, only matters of imprecise wording.

We may consider some of the examples, cited by Armstrong, in five categories (The page references refer to Armstrong's paper).

I. In some cases no reasonable evidence is given to show that the behaviour of the reactor was due to the behaviour of the actor. In the case of the male Blackbird (*Turdus merula*) (p. 55) which showed incipient building behaviour while his mate was collecting material, there is no reason to suppose from the description given that the male's behaviour was influenced by that of the female. The males of many Passerine species have the nervous mechanism necessary for nest-building behaviour, though the motivational factors are normally low (e.g., tits, *Parus*, and finches, *Fringillidae*, to cite two examples with which the present writer is familiar). Such birds may show incipient building behaviour at any time. Similarly, in the reference to Berry's (1943, 1944) record of nesting geese (p. 55), no evidence is cited to show that it was the behaviour of other individuals, rather than the presence of nesting material, which caused building behaviour.

II. A number of cases seem to fall outside the definition of mimesis. Craig's (1913) record of synchronisation in egg-laying between pigeons which could hear but not see each other (p. 55) does not show that the calling of one pair evoked "the same or a closely similar behaviour pattern" (see definition) in the other. It shows, at most, that the calling of one pair may "accelerate the sexual development" (p. 55) of the other—i.e., that it affects the whole reproductive instinct, of which calling and egg-laying are each separate parts. A similar comment may be applied to Heinroth's (1935) record of *Mareca sibilatrix*, and all the records of synchronous breeding in colonies, etc.; (p. 54/55). The evidence that the reproductive drive in one

individual may be increased through the proximity of others engaged in reproductive activities is considerable, but such cases certainly do not necessarily involve "like eliciting like" (p. 48), nor "the reproduction by one animal of the instinctive behaviour patterns of another" (p. 46). It may be that the difficulty here is partially a terminological one, and that "behaviour patterns" is intended by Armstrong to cover both particular instinctive activities (as preening) and the whole of a major instinct—a confusing use of the term. If this is the case, and "mimesis" is thus to cover such widely differing cases as "mimetically induced" preening (p. 52) and the synchronisation in egg-laying between pigeons, then the term "mimesis" is so broad as to be valueless.

III. Armstrong claims that mimesis is involved in many cases of mutual epigamic or aggressive display (p. 49, 53, 54), but in very few of such cases has an analysis even been attempted. Turning to a case more familiar to the present writer, Great and Blue Tits when fighting often engage in "displacement pecking" at buds or twigs (Tinbergen, 1937; Hinde, 1952) and it is common to see two rivals perched close together and pecking vigorously. However, if, during the course of a skirmish, one bird starts displacement pecking, the response of the other depends on the strengths and relative strengths of its own attacking and fleeing drives—displacement pecking only occurs if both are strong and in approximate balance. There is thus no question of the reactor responding "to example." Similar considerations probably apply to many other cases of "mutual" epigamic and aposematic display. This category differs only in degree from the previous one—in each case the stimulus situation produced by the behaviour of the actor effects a (relatively) "higher centre" in the reactor, who may show any one of a number of possible responses according to the internal and external conditions.

IV. The type of behaviour upon which Armstrong dwells most is what he called the "follow-up response" (p. 49). Under this heading he groups a number of cases in which one animal follows after another, which we may subdivide as follows :—

(i) Following in the predator-prey relation, and in reproductive fighting. In these cases the behaviour of the reactor is governed by a different drive (Feeding, reproductive attack) from that of the actor (Fleeing from predator,

fleeing from reproductive attack). It is only incidentally that both happen to use similar motor patterns—a predatory bird chasing terrestrial mammals, or a dog chasing gulls on the sands, uses quite a different motor pattern from that of its prey.

(ii) Following in courtship. In many cases birds engaged in sexual chases are probably activated by the same drives as birds engaged in reproductive fighting—the members of the pair each exhibit some of the characteristics of a sex rival, as well as those of a sex partner. It may be that such chases have sometimes been elaborated into mutual flights, but no such case has yet been analysed in detail.

(iii) Following in a social context. Armstrong cites cases where "flying-up" by one member of a flock evokes flying-up by other individuals. When a flock of Great Tits moves from one place to another, the movement of the flock is preceded and accompanied by "Twink" calls which bring other individuals into a ready-to-fly mood. Actual flight by any one individual may occur without further stimulus, or it may be released by a stimulus situation which may be designated as "other-bird-flying-away." The precise characters of the latter have not been analysed, but it seems highly likely that the white tail feathers play an important part. In other words the bird is not responding "to example," but to a perfectly definite and precise pattern of stimuli.

Armstrong states that in cases such as these "we are concerned with the most unspecialised type of releasing mechanism, for it is simply a matter of like releasing like." (p. 48). The expression "like releasing like" becomes meaningless when we remember that the first like must be interpreted as a certain pattern of impulses in sensory nerves, and the second as a quite different pattern of impulses in nerves leading to muscles.

In describing the manner in which Dunlin (*Erolia alpina*) associate with plover (p. 50), Armstrong says "The most plausible explanation is that it is due to the dunlin's strongly developed mimetic impulses and a similarity between the flying-up and "following" releasers of the two species." It is not clear to the present writer what "mimetic impulses" are, but it seems quite unnecessary to invoke them—the similarity between the releasers is sufficient to account for the observed behaviour.

V. Armstrong states that "It should be noted that, theoretically, what appears to be mimetic behaviour might be produced entirely by conditioning." Although no case has been analysed as yet, this is a possibility that must be taken seriously. It could well be that the mutual stimulation amongst the members of a brood to beg (p. 52/53), amongst the members of a flock to feed (p. 52), and many other cases, might fall into this category.

It is clear from the above that the records cited as examples of mimesis show enormous diversity. In some the stimulus situation produced by the actor releases a particular behaviour pattern, as suggested by the definition; and in others it evokes a higher order mood (Armstrong's term "emotive tone" hardly seems to fit the context here). Some depend on inborn responses; others, probably, on conditioned ones. In some the reactor is activated by the same drive as the actor, and in some by another. It is thus doubtful whether any useful purpose is served by grouping such varied phenomena under one heading. Indeed, it seems that the concept of mimesis, used in this way, has no real significance, for the "examples" cited bear only a superficial resemblance to each other. When such records are grouped together, it is easy to fall into the error of using rather vague terms, like "suggestibility," which, although they may be useful in a descriptive sense and seem at first sight to have a universal application, are irrelevant in any one particular well-analysed case. It is easy to use terms like "suggestibility," and even "mimesis," in such a way as to imply that the types of behaviour under consideration possess some peculiar causal mechanism, although there is no evidence for such a view (see e.g., p. 55, col. 1, and lines 36-41 and p. 56, col. 1, lines 11-13).

Finally it must be stated clearly that some of the instances cited by Armstrong do not fit readily into any of the categories used in this paper. The present analysis certainly does not show that there are no forms of animal behaviour to which the term "mimesis" (with a modified definition) may properly be applied. The matter can, however, only be investigated by careful analysis of particular cases. By collecting such a wealth of examples Armstrong has provided a highly stimulating paper, and some tentative theorising may be permissible at this stage as a preliminary to further study, but generalisations based on unanalysed cases may be misleading.

I am indebted to Dr. W. H. Thorpe for reading the manuscript, and making a number of helpful comments. I am also very glad to have had the opportunity of discussing this paper with Rev. E. A. Armstrong—the discussion did much to clarify the ways in which the approach expressed here differed from his, and helped me a great deal.

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Reply by E. A. ARMSTRONG

The Editor has invited me to comment briefly on Dr. Hinde's criticisms of my paper on "The nature and function of animal mimesis" and in doing so I would stress that its purpose was to suggest a term which would enable imitative behaviour, regarded as involving "the copying of a novel or otherwise improbable act" (Thorpe, 1950) to be clearly distinguished in discussion from a number of other forms of behaviour with which it has been, and still is, confused, and which commonly go by vague, ambiguous or even misleading terms such as "contagious" or "infectious behaviour," social facilitation, or, indeed, "imitation." As Hinde repeatedly points out, these forms of behaviour have not been analysed and therefore my treatment was descriptive rather than analytical, as such preliminary surveys must be, and my two tentative definitions very generalised. The history of "instinct" shows that for descriptive purposes a term may be given a wide or narrow extension at different periods and considerable discussion

may be necessary before agreement is reached on the range of phenomena to which it may be applied. Undoubtedly experimentation and analysis, as in all research, will result in further clarification of the concept of mimesis. It may, for example, be necessary, to establish a further differentiation of categories, such as mimetic and pseudo-mimetic, but the function of a descriptive paper is to review all the forms of behaviour which apparently come within the extension of the term suggested. A term is not shown to be valueless, nor the concept to which it refers invalidated, if its extension has later to be narrowed or its intention conceived somewhat differently.

In my paper I drew a distinction, which Hinde's criticisms do not always take into account, between mimesis, mimetic elements in behaviour and mimetic susceptibility. The mimetic element should be regarded as a proclivity towards the reproduction of the activities of a fellow. "Potentiality" in this context is inadequate, as we are concerned not merely with the organism's ability to perform certain behaviour but its constitutional bias to behave in that way. As we speak of persons being imitative so we can speak of organisms being mimetic. Because on the level of expression mimeticness employs the recognised apparatus of releaser mechanisms does not imply that, as Hinde suggests, it does not exist or that the concept is useless. We have to recognise a differentiation within the concept "drive" (Thorpe, 1951) to include proclivities.

The nature of a proclivity may be illustrated by considering behaviour which is, perhaps, on the borderland between mimesis and imitation—the reproduction of environmental sounds by birds. It is more accurate to describe a mockingbird *Mimus polyglottos* as possessing a proclivity to reproduce environmental sounds than to say it has a potentiality to do so.

A few comments may be made on specific points raised by Hinde's paper:

(i) My paper was written before the quoted definition of "releaser" appeared. The concept implies a percipient, and a subject-object relationship is always involved. However, behaviour usually correlated with an external stimulus situation sometimes occurs in its absence. The evidence that it is activated by something corresponding to an image or "internalised releaser" is considerable but this field for research has yet to be investigated (Armstrong, *In the press*).

(ii) I agree with the implication that a clear distinction between a "releaser" and a "releasing influence" cannot always be drawn.

(iii) I have endeavoured above to make my meaning clear on this point.

I. In a number of instances the necessity for brevity precluded full evidence being cited. On first being observed the male blackbird *Turdus merula* was moving here and there near the female in such an odd, tense way as to keep my attention fixed on the pair, anticipating some interesting behaviour. All those who have concentrated on studying birds intently will be familiar with such situations in which uncertain or apparently inhibited behaviour suggests that some peculiar action may follow. In the circumstances to suppose the male's behaviour uninfluenced by the female's is stretching coincidence too far. Moreover, other instances may be cited. Only rarely does a female wren *Troglodytes troglodytes* construct the nest but one was seen intently watching her mate building for some time and then starting to build (Kluijver *et al.*, 1940). In regard to the stimulated nesting of geese, if Hinde acknowledges, as he does, that the sight of nesting material may stimulate birds to build, the onus is on him to show that the sight of other birds manipulating such material is not *a fortiori* a stimulus.

II. As I have indicated above my argument is that mimeticness is the foundation for synchronous behaviour of the types mentioned.

III. In view of descriptions which I have given of the mutual display of whooper swans *Cygnus cygnus* (1946) and other birds (1947), Hinde should show that mimesis is not involved. I am not quite sure of the relevance of his example of displacement-pecking by tits but will cite an instance of a displacement-activity in which mimesis played a part. Edwards, Hosking & Smith (1948) described the attack of a female oystercatcher *Haematopus ostralegus* on a mount. Excited by this situation she displacement-bathed. Thereupon the male, who had been showing his excitement by piping, also displacement-bathed.

IV. That precise and specific patterns of stimuli are involved in "follow-up" behaviour is not in question. I have already called attention to the probable function of white feathers on rump or tail acting as "follow-up" releasers (1947). The issue is whether or not a

"following" proclivity is a characteristic of animals, particularly those which are most social. Baerends (1950) states: "The system of social releasers and releasing stimuli serves the activation of instincts in a fellow. The simplest way in which this is done is perhaps the mere imitation of the releasing activity in the other animal." For "the mere imitation of the releasing activity in" I would substitute "mimesis of the releasing activity by" the other animal.

V. I must again voice a protest against such phrases as "a higher order mood." Ethology should not appropriate terms saturated with psychological significance to designate other states or situations.

Hinde's admission that a number of the instances cited in my paper do not fit into his categories suggests that they are inadequate. He does not advance any alternative term or set of terms to alleviate the confusion due to the current use of unsuitable terms. His contention that the attempt to improve on this state of affairs must await the careful analysis of the wide

variety of phenomena I have cited is a counsel of despair.

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The Critical Approach in Grazing Behaviour Studies*

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Since the meeting organised jointly by this Society and the British Society of Animal Production in 1944 the importance of animal behaviour studies in agriculture has gained general recognition. It is encouraging to find that whereas in 1944 such studies were the preserve of a minority of enthusiasts, who managed to include them unofficially in a quite different programme of research, we now have groups of workers in many agricultural research institutes and universities tackling behaviour problems with the official blessing of the authorities. It is the purpose of this symposium to review the progress that has been made during the last six years in order that, by discussing results already obtained, workers might be in an improved position to plan and execute future projects. However before these detailed results are discussed we wish to indicate one or two points of principle and method that we have found to be extremely important while carrying out work at the Rowett Research Institute.

Edwards (1944) has shown how the general study of animal behaviour has developed in three phases. Firstly there was the *Anecdotal Period* which produced many observational reports the value of which was greatly diminished by a tendency towards anthropomorphic interpretation. Then followed the *Experimental Period* during which animals were subjected to a variety of stimuli under conditions far removed from their ecological norms. Clearly the results of this period have had a greater influence on the development of such sciences as physiology than on that of ethology. Finally the *Modern Period* emphasises the importance of careful observation and experimentation with animals in their "Natural Setting" and an equally careful interpretation of results. As Russell (1938) has stressed we must distinguish between facts and interpretation, and while any straightforward and accurate description of animal behaviour is useful, much of the value is lost if it is "wrapped up in a bundle of faulty interpretation." Since the object of animal behaviour studies is a fuller understanding through the animal's actions of the under-

lying causes the emphasis on careful interpretation is clearly wise, although what constitutes a "correct interpretation" must necessarily remain a matter for experiment.

The development of studies which have to deal with domestic animals in general, and grazing domestic animals in particular, has one important similarity to, and one important difference from other animal behaviour studies.

Firstly, let us consider the similarity. As with general studies in behaviour, the beginning of grazing studies may be described as the *Anecdotal Period*. While many valuable observations have been recorded the interpretations of them have often inclined towards anthropomorphism (see e.g. Stapledon, 1948a; Thomas, 1949). Those who have led the way in stressing the importance of a knowledge of grazing behaviour have unfortunately also stressed that not only does an animal require the fulfilment of certain nutritional and physiological conditions but that "he knows he does" (Stapledon, 1948a). This belief leads to the proposition that the ability of a cow to produce to its optimal capacity depends upon its welfare which in turn is reflected in its grazing behaviour. This implies that we may use grazing behaviour as the criterion of a system of grassland management. As has been indicated elsewhere such a proposition requires critical examination (Hancock, 1950; Tribe, 1950).

Recorded observations show that cows grazing leys of a few species of grasses and clovers frequently make determined efforts to eat the indigenous plants in neighbouring fields and hedgerows (Davies, 1948). Similarly we know that if given access to widely differing types of vegetation grazing animals will "roam and graze in patches" (Stapledon, 1948a), selecting not only the luscious young herbage but also the more fibrous and mature plants which are commonly designated "weeds." To claim on

* The opening paper at a "Symposium on Grazing Behaviour" held at the Zoological Society, London, on 13th January, 1951. Further papers from this symposium will be published in this and subsequent issues.

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the basis of such observations that the animal is searching for a particular nutritional balance is dangerous. Such a claim must obviously have experimental verification before it can expect recognition.

In a recent paper on the importance of weeds for the nutrition of cattle, von Gruenigen (1949) suggests that the absence of herbs, known to be rich in minerals and trace elements, from the pastures consisting of only a few species of grasses and clovers, may lead to deficiency diseases in the cattle, and particularly calves, grazing them. It is well known that under certain conditions such as those existing in the Solway Firth the cobalt content of pastures may be so low as to produce a deficiency in sheep (Stewart, 1946), and in Caithness, Jamieson & Allcroft (1950), have shown that cattle suffer from a hypocupraemia although the cause is not yet understood. These conditions, however, are certainly exceptional and, in any case, cannot be cured by merely offering the cattle a wider range of vegetation. That mineral and trace element deficiencies are unlikely to occur under normal ley conditions is shown by the following examples.

A sheep weighing one hundred and sixty pounds will consume about five pounds of dry matter per day when grazing average pasture (Woodman, Evans & Eden, 1937). By taking the figure quoted by Halnan & Garner (1944) of 0.28 percentage CaO in average pasture grass, and substituting it in the above figures it appears that sheep on such pasture will consume 6.3g CaO. The requirements of a one hundred and seventy-five pound sheep have been given as 4.9g CaO per day (Report, 1949), and this is generally considered to be rather high. Therefore the animal weighing 160 pounds would require no more than 5.0g CaO when at pasture and would consume 6.3g. Doubtless there are errors in such calculations and these last figures certainly cannot be taken literally, but they serve to show that it must be under very abnormal conditions that grazing animals suffer from a calcium deficiency, and these conditions are not likely to occur in modern leys.

Similar calculations for the intake of phosphorus by cows have been made by Cunningham (1947) who shows that a pasture containing 0.7 per cent. of phosphoric acid, on a dry matter basis, supplies more than enough phosphorus for a cow producing three gallons of milk daily. Figures published by the Ministry of Agriculture

(Woodman, 1948) show that average pasture grass in this country contains 0.8 per cent. phosphoric acid.

Again, if cobalt is taken as an example of the trace elements it can be calculated that a sheep weighing one hundred and sixty pounds would eat 4.5 mg. of cobalt daily while its requirements would be more than covered by 0.5 mg. of cobalt (Lines, 1935; Askew & Dixon, 1936).

From these calculations it certainly does not appear likely that animals grazing leys suffer any risk of mineral or trace element deficiencies. In any case the general supposition that an animal's appetite behaviour is an infallible guide to its nutritional requirements has been shown to be false (Scott, 1948; Tribe & Gordon, 1950), and in this connection an experiment by Cunningham (1949) is particularly impressive. He managed two similar groups of sheep on similar pastures and gave them equal opportunity to eat a mineral lick. The sheep in one group, however, were given each day through a stomach tube 10g. of the lick suspended in water while the others were given the water alone. It was found that over a four-month period the group which was dosed with the minerals voluntarily consumed an average of 4.7 g. per day of the lick in the field while the undosed sheep consumed an average of only 3.8 g. per day. This is good evidence that the appetite behaviour of an animal does not necessarily reflect its nutritional status.

To determine whether the presence of widely differing types of herbage makes any difference to the body weight increase of young Ayrshire cattle we recently carried out the following experiment. Two groups, each of eleven specially selected animals, were grazed on two four-acre plots from March to October, 1950. One plot contained only the grasses and clovers commonly advocated for three-year leys in the North of Scotland and were mostly Aberystwyth strains of ryegrass, cocksfoot, timothy, red and white clovers. Great care was taken to ensure that this area was as weed free as possible and it was both sprayed and weeded by hand. The other plot contained three and a half acres of precisely the same mixture, while the remaining half acre was sown with as wide a variety of weeds as could be obtained. This plot also contained some shrubs such as *Ulex europaeus* and *Cytisus scoparius* and thus presented to the animals a wide range of plant species in various stages of maturity. At no time did the weight

increases of the groups vary significantly although the animals having access to the weeds certainly grazed them very readily. These results certainly do not show that the weeds did not give the animals grazing them a feeling of greater comfort and well being than those on the other plot, but, since their growth performance was the same, they suggest that there can be no nutritional merit in offering such animals vegetation of widely differing types. Of course it may be said that pregnant or lactating cows would have behaved differently, but since the chief merit of weeds is said to be their mineral content (von Gruenigen, 1949), the use of young grazing animals, whose mineral requirements are known to be high, should have been sufficient to demonstrate the value of weeds.

This experiment leads naturally to the difference between grazing, and general behaviour studies. We have already stated that the object of the latter is a fuller understanding through the animal's actions of the causes underlining them. The object of grazing behaviour studies with domestic stock is, however, an increased efficiency of animal production. It may be legitimately argued that a fundamental understanding of behaviour will ultimately lead to improved methods of animal management for optimum production since "a fuller knowledge gives a fuller control." However, it must be remembered that this is not the only way of gaining a "fuller knowledge," and, from a short term view at any rate, it is probable that other types of animal experimentation will give better dividends in terms of animal production. This does not mean that behaviour studies have no application in animal husbandry in the near future. When carrying out animal production trials it is frequently necessary to make behaviour observations before the results obtained are fully understandable. The work of Levy (1935) and Nichols (1944) are obvious examples of this. As an appendage to a managerial investigation, behaviour studies may often be invaluable, but as independent investigations their bearing on animal husbandry is at present limited.

The results obtained from independent animal watching studies have an inductive rather than a deductive value. They give rise to much speculation on the wide issues of animal husbandry and nutrition, and provided they are followed by an experimental phase they may provide a powerful stimulus to agricultural

research and practice. If, however, the experimental phase is neglected and speculations are regarded as certainties then research and practice will be retarded rather than stimulated.

With general behaviour studies it is the aim of the observer to watch his subject in its "Natural Setting," or, as it is better called, its ecological norm, but the modern cow and sheep are dependent upon the environmental conditions imposed by man. Such man-made environments differ widely both generally and in detail. It is our job not to preserve what appears to be the most favourable environment as judged by an animal's behaviour, but to devise an environment which gives optimal animal production, remembering, of course, that longevity, fertility, and the effect on the performance of the progeny of treatments administered to the parents are all important factors in animal production. Experimental evidence to show that these environments are not necessarily identical will be presented later by Corbett (1952).

To sum up we can say that :

(a) The behaviour of a grazing animal does not necessarily reflect its nutritional and physiological requirements. It is therefore unwise to base a system of animal management on recorded observations of behaviour.

(b) The essential criterion to use when comparing the efficiency of different systems of animal management must be animal production. For a complete and critical appreciation of production records, however, it is essential to have a knowledge of the quantity of herbage consumed, by the grazing animal together with a record of its behaviour.

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The Grazing Behaviour of the Wild Rabbit, *Oryctolagus Cuniculus* (L.)*

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1. Introduction

Individual rabbits living wild cannot be continuously observed as readily as cows and sheep (Johnstone-Wallace, 1938; Tribe, 1949) and, although observations on behaviour *sensu strictu* are being accumulated, most of our information on grazing behaviour is deduced from the influence of rabbits on the vegetation. The first extensive description of this influence is contained in the now classic publication of Farrow (1917) who showed how an area of *Calluna vulgaris* was killed by rabbit grazing and succeeded by a grass-heath association. In extreme cases the grass-heath was replaced by lichens. Tansley & Adamson (1925) found that intensive rabbit grazing of chalk grassland reduced the herbage to 2 c.m. and usually eliminated mosses (presumably because of dryness). Conversely, on steep north slopes shadow mosses are luxuriant, since uneaten by rabbits. Thomas (1937) has shown that when rabbits are kept continuously on small plots the useful grasses and clover are eliminated and replaced by weeds and mosses. The vegetation of certain hill grazing districts in Scotland has been profoundly modified by rabbits (Fenton, 1940), a heath-grassland sheep-biotic-climax being eventually replaced by a moss-lichen rabbit-biotic-climax.

2. Grazing of Pasture

It may be considered that rabbits grazing near their burrows do not do a great deal of damage, particularly in hill grazings, but the total effect of a number of colonies is clearly considerable. Damage to pasture is less obvious than that to arable crops, although disturbance of the soil surface by rabbits assists in the establishment of the conspicuous ragwort, *Senecio jacobaea* (Cameron, 1935).

An interesting study has recently been made by Phillips (in preparation) in Cardiganshire. A pasture was directly reseeded with a mixture of perennial and Italian rye grass, red and white

clover, and rape. Two one-acre plots were fenced with rabbit-proof wire and two with pig-netting wire. The herbage was controlled by lambs for a period in the autumn of the sowing year and in the following spring.

The general effect of the grazing on the pasture was to cause a marked reduction in the yield of total herbage (as determined by sample cuts and plant counts), particularly of the sown species, while there was an increase in the yield of weeds. The rate of growth of the herbage and the feeding value of the pasture in terms of lamb live weight increment were also adversely affected.

Rye grasses were eaten by rabbits in preference to clover and rape; Italian rye grass was more palatable than perennial.

In collaboration with Wye Agricultural College, Thompson & Armour are conducting an experiment similar to that of Phillips; the main differences being (a) that it is on permanent chalk grassland, as compared with siliceous reseeded pasture, and (b) that the emphasis is upon the number of sheep displaced by a population of rabbits, rather than on herbage analysis.

An area of six and three-eighths acres has been surrounded by a rabbit proof guard fence, inside which is a rabbit warren of three-quarter-acre cut off by rabbit proof netting from six plots of just under one acre each. From the warren the rabbits have access to three of the six plots through nine tunnels let into the netting.

Sheep are grazed for two-three week periods, followed by two-three week rests, through spring, summer and autumn, and herbage samples are cut from inside and outside rabbit-proof cages before and after each grazing period. It is thus possible to calculate the herbage eaten by the sheep on the rabbit-free plots, and that eaten by rabbits when alone and rabbits and sheep when together on the rabbit-grazed plots. Records are kept of the numbers of sheep maintained on the plots and increases in their weight. Botanical changes in the

* Presented on 13th Jan., 1951—see footnote to p. 12.

sward of each plot are being studied and rabbits are periodically live-trapped, marked, weighed and watched through field glasses and a telescope. During the first seven months of the experiment (May to November, 1950) the sheep live weight increase on the rabbit-free plots has been 800 lb. and on the rabbit-grazed plots 650 lb.

3. Grazing of Arable Crops

Damage to market garden crops, mangolds and sugar-beet, kale, cabbage and lucerne are well known, and grazing of cereals is especially serious. Members of the National Agricultural Advisory Service are well aware of the importance of this damage and the attention of some of them has been drawn particularly to the grazing of winter cereals (Gough & Dunnett, 1950). Entire fields of winter wheat or oats may be grazed down to the ground in a few weeks or even days, and the number of plants so reduced that re-sowing is necessary.

While rabbit damage to spring cereals is less catastrophic, and more localized in its incidence, it may nevertheless seriously reduce the crop. A recent pilot survey of the damage to spring wheat in Kent (Thompson, Jolly & Armour, in the press) was made by erecting 38 pairs of 5 yd. x 5 yd. plots, one of each pair being rabbit-proofed, and the other unproofed, in randomly selected fields. A four square yard sample was cut from the centre of each plot at harvest and the grain threshed and dried to constant weight. In most cases there was a substantial difference in yield in favour of the fenced plot. The mean difference for the county was 2.95 cwt. per acre (± 0.69 cwt. per acre) or about one-sixth of the average yield of the fenced plot.

4. Damage to Trees

Rabbits are a source of great anxiety to foresters, preventing natural regeneration by eating seedlings, distorting the growth of trees by damaging leading shoots (Watt, 1919; Forestry Commissioners, 1943), and killing trees by ring-barking. Orchards are particularly vulnerable especially when pasture is scarce, and in a test of rabbit-repellent substances currently taking place at Wye, Kent (Thompson & Armour), 41 out of 44 control (untreated) apple rootstocks have been gnawed by rabbits within the first six weeks of the experiment.

5. Observations of Behaviour

Grazing is interspersed with other activities such as washing, basking in the sun, just sitting, and sexual and territorial behaviour. A varying amount of alertness is displayed by rabbits on different occasions; sometimes the sound of a tractor in a neighbouring field will send them all to earth, whereas on another day the tractor excites no reaction.

Movements of the ears vary continually during grazing. Much of the time they are lying backwards but, periodically, either the left or right ear is erected and faced forwards. Occasionally both ears face forwards, but usually only when some sight or sound appears to have made the rabbit unusually alert, when it ceases cropping, raises its head and looks round. We have not noticed any rabbit of a grazing group to act as sentinel, although at any moment one or other of the rabbits may happen to be more alert than the others. Despite their communal habit, there seems no justification for supposing the existence of a community spirit among rabbits.

Most grazing occurs round the burrows, where the herbage is kept extremely short, but rabbits may use a total feeding area covering several acres. They appear to take fright easily when grazing far away from their burrows.

As already noted by Southern (1940) feeding may be "casual," usually near a burrow entrance—rabbits have been seen to lie for an hour or more in one position taking an occasional nibble—or "normal." Normal feeding is true cropping, usually on hard-grazed areas. In the normal feeding observed by Southern an area of a semi-circle was cropped by the animal moving its head from side to side. It then moved forwards in a new direction—in which it happened to be facing—and so described a zig-zag path. While we have observed this zig-zag progression at Wye (Thompson & Armour, unpublished), the more usual behaviour of our rabbits is to graze in a semi-circle (say 9.00 o'clock to 3.00 o'clock and back again several times) then to return the head to 12.00 o'clock and hop or shuffle forwards six to nine inches and crop again, *i.e.*, they move forwards more or less in a straight line. We have made only a few observations of the movements of the rabbit's jaws in cropping but they are rapid, averaging 120 per minute.

Rabbits feed throughout the day at Wye in spring, summer and autumn, but are seen in

larger numbers from dawn to 7.00-8.00 a.m. and from about 5.30 p.m. to sunset, i.e., when human activity is least. Although they are difficult to observe at night, we know that rabbits feed during the hours of darkness, since they may be seen by moonlight and flashlight, and are found to have full stomachs when caught in gins, snares and live-traps; while their tracks are numerous in overnight snow.

Rain

Although they are not disturbed by slight rain, rabbits dislike grazing in heavy rain and retire to their burrows. When the herbage is wet from dew or rain, a habit of licking and then "fluttering" the forepaws has been frequently observed, presumably to shake off excess moisture. Sitting back on its hind legs, the rabbit holds its forepaws out in front of it and flicks them rapidly up and down in opposite directions, chiefly by wrist movement.

Temperature

Cold does not seem greatly to affect feeding unless combined with wind. Sunshine, however, will stimulate non-grazing rabbits to feed and grazing rabbits to start basking or washing; this is particularly noticeable in the early morning.

Wind

Feeding activity decreases in any cold wind, particularly if from north or east. Rabbits lie close to the ground with their ears flattened back. Sometimes they shelter from the wind and graze in the lee of nettles or in depressions in the ground.

Snow

A strong wind and snow keeps rabbits underground, but they will graze when snow is falling if there is little wind. Damage to trees increases when snow is on the ground and the consumption of herbage decreases. Only a few observations of rabbits cropping snow-covered herbage have been made. They remained for many minutes in the same bodily position, cropping steadily, the movements of the head being less lateral than usual; then either made slow progress forwards more or less in a straight line, or moved by hops to areas where grass showed through the snow. When eating, snow was cleared from the region of the mouth either by quick alternating movements of the

forepaws, or by pushing it away with the nose. Such grazing resulted in snow being cleared from patches of ground about 9 inches x 6 inches.

A fairly complete list of plant species not grazed by rabbits is given in Tansley (1939). On the warren at Wye the observation first recorded by Jeffreys (1917), and many others since, that *Urtica dioica* is not usually eaten was confirmed. However, rabbits were observed eating the stems of nettles cut the same day and, three days later, two young rabbits were seen feeding on the leaves. Each young rabbit showed obvious discomfort, pausing every few seconds to rub its mouth with its forepaws and to press each forepaw in turn against the ground and rub it with the other. Other completely rabbit-resistant species on the warren are *Nepeta hederacea* and *Bryonia dioica*. *Brachypodium pinnatum* is grazed by rabbits but less so than other grasses such as *Agrostis vulgaris* and *Festuca ovina*. Fenton and others have found *Digitalis purpurea* to be grazed when the leaves are young, and also *Deschampsia flexuosa*, *Nardus stricta* and *Vaccinium myrtillus*. Southern has observed rabbits feeding on *Arctium lappa* and *Ranunculus bulbosus*.

The importance of the rabbit as a competitor of domestic stock for pasture and a destroyer of arable crops and trees makes a knowledge of all aspects of its behaviour a matter of some moment, despite the real difficulties of obtaining accurate information.

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Sex Hormones and Human Behaviour*

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It seems clear that during the process of phylogenetic development the higher species have become less dependent on well-defined neurogenic and hormonal stimuli in their sexual behaviour, and that this is more and more determined by fashion, custom and psychogenic influence (Beach, 1947). This fact, alone, makes it extremely difficult to analyse in any scientific manner human sexual behaviour.

Furthermore the clinician is at a disadvantage in comparison with his biological colleagues, in that he is unable to keep his "animals" under experimental conditions in order to observe their sexual behaviour in a purely scientific manner and must rely upon their own account, and even if this is recorded with the meticulous exactitude of the Kinsey Report a lot is left to the imagination.

In this brief review of behaviour in the human subject the action of sex-hormones in precocious puberty, in gonadal deficiency and castration, in the normal individual and in the homosexual will be considered.

Precocious Puberty

In the *male* precocious puberty occurs in cases of adrenal cortical tumour, interstitial cell tumour of the testis and lesions of the posterior hypothalamus. In every case the increased 17-ketosteroid output indicates an excess of androgen activity though it is only in the patients with testicular tumours and hypothalamic lesions that the excessive androgen is derived from the testis. In each of the three types of case the precocity embraces libido, and in many juvenile patients considerable embarrassment has been caused by the precocious sexual advances. In these cases, therefore, undoubtedly the testosterone secreted by their precociously advanced testes, as well as the adrenal androgens secreted in the cases of adrenal cortical tumour, are capable of inducing normal adult male sex desire.

Precocious puberty in the *female* is usually

constitutional though it may on rare occasions be due to a granulosa cell tumour of the ovary, hypothalamic lesions or Albright's syndrome of polyostotic fibrous dysplasia, pigmentation and precocity (Albright *et al.*, 1947). Adult sexual behaviour is not a conspicuous feature, though cases of pregnancy have been recorded. "La plus jeune mère du monde" was a Peruvian child of five years six months, who developed sexually and menstruated at the age of three (Wilkins, 1950). She was delivered by Caesarian section of a baby boy weighing 6½ pound. She was a case of constitutional precocity. Her pregnancy need not, of course, have been the result of precocious libido. Precocious virilism results from prepubertal adrenal cortical tumours, but precocious sexual behaviour, either isosexual or heterosexual, is not a conspicuous feature.

Sexual Behaviour Patterns in Normal Adults

It is difficult to determine, from the existing evidence, whether the adult male of the human species is more dependent on neurogenic and hormonal stimuli of endogenous origin than on social convention, as compared with the adult female. Certainly there is no evidence of cyclical variation in gonadal or adrenal cortical secretion in the male nor does there seem to be any rhythm of libido, though the sexual urge may be present from puberty to an advanced old age, and may be strongly marked during adolescence (Kinsey *et al.*, 1948).

In women there is of course a cycle of secretion of the ovarian hormones and at different times during this cycle first one then the other ovarian hormone predominates in its influence on the endometrium, the vaginal mucosa and so on. It is however doubtful whether the cyclical activity of the ovary affects the behaviour of the woman. It has been suggested, chiefly in psychiatric circles, that well-marked and characteristic changes in mood do indeed occur throughout the various phases of the cycle, with increasing receptivity associated with coquettishness and a tendency to flirt in the pre-ovulatory phase of the cycle which is in marked

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contrast to the development of the maternal and nesting instinct in the luteal phase. Personally I remain a little sceptical. Though this attractive and interesting theory should be accepted with caution the "nesting" instinct does seem to be evident in some women towards the end of their pregnancy, though this may represent merely a conscientious reaction to practical necessity rather than a manifestation of some endocrine influence. One dramatic and well-recognised change of mood which may occur is the syndrome of premenstrual tension associated with headaches, tenderness of the breasts, abdominal swelling and bloatedness, and often extreme irritability. Almost certainly this is the effect of circulation of menstrual toxin in excessive concentrations. Small doses of androgen are often effective in relieving the symptoms.

Sexual Behaviour in Cases of Gonadal Deficiency.

In the Male

Failure of gonadal development is more common in the male than in the female and eunuchoidism becomes obvious during adolescence. It is usual to find both at this time and later when manhood is attained that the opposite sex is shunned. Undoubtedly this is largely due to embarrassment of these individuals at their obviously youthful and eunuchoid appearance; it is partly due, however, to the diffidence, lack of initiative and aggressiveness which is a characteristic feature. This peculiar characteristic is most dramatically brought out by studying the effects of androgens in these cases. In this connection the story of the "peck order" is pertinent. Twelve hens, all strangers to one another, were brought together in the same pen. Within a short time they arranged themselves in peck order. No. 1 henpecked all the other hens, and No. 12 hen was pecked by the rest. No. 12 hen was then injected with testosterone and soon assumed position No. 1 pecking all the other hens. This characteristic of male aggressiveness is a well marked result of treating eunuchoids with androgens, and it may be this development of initiative and "drive" which prompts the treated eunuchoid to approach the opposite sex. Nevertheless the untreated eunuchoid is grossly lacking in sexual power, and erections and emissions are infrequent or absent. It is a popular belief that the male castrated in adult life may experience no diminution in

sexual urge and remain potent. This has not been my experience with these cases. I have a number of patients whose testicles have been removed on account of war wounds or tuberculosis epididymitis. Apart from the intense and almost constant hot flushes, and the marked asthenia and muscular weakness from which they suffer all of them have become impotent. They are all under periodic treatment with testosterone implants, which remain effective for five to six months and it is often their gradually increasing impotence which brings them back at the end of this time for another implant.

In the Female

Since the sexual role of the female is more passive than that of the male the effects of gonadectomy are far less marked. Furthermore complete gonadal failure is rare in girls. On the other hand bilateral oöphorectomy is performed surprisingly frequently in women suffering from various gynaecological disorders. Distressing symptoms often follow this artificial menopause, such as intense hot flushes and night sweats, profound depression and involutional melancholia: nevertheless these are seldom strongly associated with sexual feelings and loss of libido and frigidity are not marked features. These are, however, merely clinical impressions. Recently at the Chelsea Hospital for Women we have conducted a follow-up study of over 300 women who had undergone hysterectomy. In those cases in which both ovaries had been removed at the same time, all complained of menopausal symptoms following the operation: where there had been partial interference with ovarian function 50 per cent. complained of menopausal symptoms, and in those cases in which only the uterus was removed 25 per cent. subsequently showed evidence of ovarian deficiency, probably owing to interference with the ovarian blood supply. Of the whole series however the surprisingly large proportion of one-third complained of loss of libido within a short time. It would therefore seem that oestrogens may play an important part in female sexual behaviour though the relatively passive role which the woman assumes in sexual relationship makes it difficult to assess at all accurately the influence of the female sex hormone. Following the natural menopause, for instance, many women show no diminution in sexual receptivity, nor does the administration of even large doses

of oestrogen to the post-menopausal woman usually increase libido.

The Administration of Sex-Hormones to Normal Individuals

Klein (1952) has made some interesting observations on sexual behaviour in rats. Ovariectomised female rats were put in a cage with a sufficient number of male rats to ensure their complete sexual gratification. The frequency of reception was low. If treated with oestrogen there was no improvement. Progesterone did not affect sexual behaviour, but androgens increased the number of times the female would accept the male markedly. This is also the clinical experience with normal women. Large doses of androgen induce swelling and vascular congestion of the clitoris and labia majora, and it might be supposed that this mechanical effect accounts for the efficacy of treatment in some cases of frigidity. But this is not the case. In the absence of such local changes androgens seem to increase sexual desire in the normal female. Foss (1951) has drawn attention to this in cases of cancer of the breast treated with large doses of androgen. In the normal male, however, it is doubtful whether androgens improve sexual performance. Most cases of impotence are considered to be psychological in origin and seldom show any physical signs of androgenic deficiency. In these cases, especially when they occur in young men, androgen therapy rarely relieves the condition and when it does it is probably on account of its psycho-therapeutic effect. There are, however, cases such as we have seen at our Fertility Clinic at Chelsea where the wife fails to become pregnant because the rather elderly husband is unable to achieve intercourse more than once in every two or three months. Administration of androgens to these husbands has often increased the frequency and strength of erections and led to intercourse occurring more often. Furthermore in men of middle or elderly age impotence may gradually develop, though they have previously led an active sexual life. These are also occasionally assisted by androgen therapy. Here again a psychological element may be present, and androgen therapy may merely be a form of psychotherapy. We have, however, seen a sufficient number of men who have benefited from this form of treatment to feel that we are justified in applying it *faut de mieux*.

Certainly oestrogens administered to the normal male in high doses lead to impotence and loss of libido, probably through inhibition of pituitary gonadotrophins and especially the luteinising or interstitial cell stimulating hormone. This treatment has been applied to the homosexual male. Though it prevents any form of sexual practice it does not alter his sexual inclinations. Indeed there is no evidence that homosexuality is primarily an endocrine problem, or that the homosexual shows an abnormal pattern of sex hormone excretion.

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Studies in the Behaviour of Dairy Cows at Pasture

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New methods of grassland management call for more information about the grazing behaviour of the dairy cow. Trials were therefore conducted at Henley Manor Farm, Crewkerne, Somerset, using dehorned Ayrshire cows in milk.

There were at least two main reasons why this field should be investigated. Firstly, in large-scale grassland experiments, when the dairy herd is grazing one field during the day-time and another at night, it is desirable to have some information on the proportions of the daily requirements of the dairy herd which are contributed by the "day" and "night" paddocks respectively. Secondly, under conditions of intensive grazing, particularly close folding with the electric fence, an adequate water supply is essential, and it was therefore of interest to find out how often, and at what hours, a dairy cow generally drinks water.

It was appreciated that in order to be of any real value, the work must be carried out under natural conditions, and that the daily life of the dairy cow should not be disturbed in any way. One cow was selected for each study, and was kept under observation by one observer for a period of 24 hours. The trials commenced at 2.30 p.m. when the dairy herd entered the yard for the afternoon milking. During the 24 hour period, the cow under observation was allowed to mix with the remainder of the herd and to walk about the field at will. The observer followed the cow at a reasonable distance, and every effort was made not to disturb her, or the herd, in any way. During the hours of darkness, when the cow under observation was resting, it was possible to remain in a position fairly near to the animal without causing disturbance. At such a distance the jaw movements could be heard quite distinctly when the animal was ruminating but an electric torch was flashed at intervals in order to ascertain the exact times when rumination started and finished. The electric torch was also necessary when the animal proceeded to graze during hours of darkness.

The various activities of the cow were recorded

to the nearest minute in a complete time-table. For instance the exact time at which the cow started to graze was noted and also the time when grazing ceased so the total number of minutes spent grazing during the 24 hours was obtained.

The atmospheric temperature was recorded at 30 minute intervals from a thermometer carried by the observer. A note was also inserted to indicate the general weather conditions at half-hourly intervals.

Within reason any action which it was thought might throw light on the various activities of a dairy cow was recorded. The type of grazing sward, the milk yield at each of the two milkings, the number of times the cow drank water, urinated and defecated were all noted and so each complete record was built up.

As far as possible the trials were conducted at monthly intervals during the grazing season. Ideally several studies should have been conducted on a number of cows during the same 24 hours period and the procedure repeated at intervals. This was impracticable so in 1949 the first three trials were carried out on the same cow and towards the end of the season two other cows were selected, one because it was giving a fairly high milk yield, while the other was a random choice. In 1950 three trials were conducted on the cow observed in 1949 and two trials on a second cow at alternate monthly intervals.

In the results and discussion liberal use is made of the terms "day" and "night" periods. These refer to inter-milking periods and not to hours of daylight and darkness. The hours of milking were 6 a.m. and 3 p.m. and the "day" period as used in this paper means the actual number of hours and minutes from the time the cow under observation was milked in the morning until it was milked again in the afternoon. Similarly, the "night" inter-milking period is the time between the afternoon and morning milkings.

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Description of Swards Grazed

Study No. 1—6th-7th May, 1949.

The grazing field was a timothy/meadow fescue/cocksfoot ley and was used by the dairy herd during both the "day" and "night" inter-milking periods. It was strip-grazed using the electric fence and a botanical analysis of the sward gave the following results :—

Clover	75%
Cocksfoot	10%
Timothy	8%
Meadow Fescue	5%
Other Plants	2%

Study No. 2.—10th-11th June, 1949.

During the "night" inter-milking period the dairy herd was strip-grazing a field of permanent pasture by means of an electric fence. The herbage was rather mature with much of the cocksfoot and meadow foxtail in the haystage. A botanical analysis carried out during the last week in May gave the following figures for the more abundant species :

Perennial Ryegrass	15-20%	Fescue	15-20%
Wild White Clover	10%	Cocksfoot	15%
Bent and M. Foxtail	15%	Weeds	15%

During the "day" period the cows grazed the ley described in Study No. 1, when it was being strip-grazed for the second time. Some of the cocksfoot and meadow fescue had already run to seed and there was also a dense population of clovers.

The herbage was dry in both fields during the period of the trial.

Study No. 3—1st-2nd July, 1949.

During both the "day" and "night" inter-milking periods the dairy cows had access to two grazing fields, one a 3-year Cocksfoot ley and the other a field of permanent pasture. A botanical analysis in May gave the following figures :—

Ley.		Permanent Pastures.	
Clovers	30%	Perennial Ryegrass	45%
Cocksfoot	60%	Cocksfoot	10-15%
Weeds	10%	Clovers	10-15%
		Fescue	10%
		Yorkshire Fog	5-10%
		Weeds	5-10%

The herbage in both fields was dry throughout the 24 hour period. The trial was conducted during the peak of the 1949 drought and there were a number of brown areas in the field of

permanent pasture. The cocksfoot ley was strip-grazed and the run-back was very slow in recovering.

Study No. 4—28th-29th July, 1949.

The dairy herd was grazing a 10 acre field of permanent pasture; grazing was extensive and the following table gives the botanical analysis of the sward in June :—

Perennial Ryegrass	40-45%	Bent and M.	
Cocksfoot	- 5%	Foxtail	5%
Timothy	5-10%	Yorkshire Fog	10%
Poa spp.	10%	Clovers	5-10%
Other Plants	10-15%		

Study No. 5—31st August-1st September, 1949.

During the "night" period the cows grazed a field of permanent pasture; a botanical analysis carried out in May gave the following results :—

Perennial Ryegrass	5-10%
Fescue	5-10%
Yorkshire Fog	15%
Bent and M. Foxtail	25%
Clovers	5%
Weeds	30-35%

The "day" paddock was the field of permanent pasture described in Study No. 3.

It was observed that the cow selected a number of weeds. This was true of Creeping Thistle when the cow deliberately paused in its grazing activity to eat young thistles on six different occasions.

Study No. 6—21st-22nd April, 1950.

The herd was strip-grazing a ley consisting of H.1 Ryegrass and Broad Red Clover in its first year when it was used for "early bite." An analysis showed that the sward contained 73% Ryegrass and 27% clover.

It was obvious during this trial that the cows preferred to eat the tips of the leaves before starting on the remainder of the grass shoots.

Study No. 7—26th-27th May, 1950.

The "night" paddock was a 10 acre field of permanent pasture grazed extensively. A botanical analysis carried out in May gave the following figures :—

Perennial Ryegrass	10%	Fescue	5%
Cocksfoot	5%	Poa spp.	5-10%
Timothy	Tr.	Bent and M.	
Clover	5%	Foxtail	45%
Yorkshire Fog	5-10%		

The "day" paddock was a three year Cocksfoot ley, strip-grazed, consisting of :—

Cocksfoot	40%
Clover	50%
Weeds	5-10%

Study No. 8—23rd-24th June, 1950.

During the "night" period the cows were strip-grazing the three year ley described in Study No. 1. The botanical analysis of the sward in May, 1950, was :—

Clovers	70%	M. Fescue	10%
Cocksfoot	10%	Weeds	5%
Timothy	5%		

The "day" paddock was a seven acre field of maiden seeds grazed extensively.

Study No. 9—20th-21st July, 1950.

The dairy herd was strip-grazing a direct re-seeded Timothy-Ryegrass ley during both inter-milking periods. Part of the field which was unploughable represented the old permanent pasture but owing to the time necessary for the proper establishment of the new ley this was in the "hay" stage and was coarse and fibrous for grazing. During the trial the herd had access to both the new ley and the permanent pasture.

The herbage was lush and leafy, with ryegrass dominant, approximately nine inches in height. It was observed that the cow under observation did not graze the strip of permanent pasture at any time.

Study No. 10—23rd-24th August, 1950.

The "night" paddock was the ley described in Study No. 6 which was again strip-grazed, while the "day" paddock was the permanent pasture described in Study No. 7, grazed extensively.

Results and Discussion

Table I is a summary of the 10 trials showing the grazing hours, the time necessary for chewing cud and other incidental factors such as atmospheric temperature, condition and length of herbage, milk yield and so on. The total time spent grazing ranged from 5 hours 39 minutes to 7 hours 49 minutes, giving an overall average of 6 hours 58 minutes, or nearly 7 hours. The time occupied in chewing cud varied from 4 hours 18 minutes to 9 hours 12 minutes, giving an average of 6 hours 18 minutes.

Table II gives the same information for the six studies conducted on one cow.

The hours of grazing and chewing cud have been split into "day" and "night" inter-milking periods thus showing the amount of time spent grazing and cudding when the cow was in the "day" and "night" paddocks respectively. The figures for grazing may therefore serve as an indication of the proportions of the daily requirements of the animal which were obtained from the "day" and "night" paddocks. The average figures in Table I show that in 1949 the animal obtained 36% of its requirement from the "day" paddock and 63% from the "night" paddock whereas in 1950 each field provided almost 50%. The corresponding figures in Table II, which are for one individual cow, are in close agreement but there is considerable variation in the figures for individual trials.

It was observed during the 1949 trials that the animal preferred to graze under relatively cool weather conditions and rest during periods of high temperatures. In the warm summer of 1949 the time spent grazing during the "day" period was less than under the cooler conditions which prevailed during the summer months of 1950. Weather conditions appeared to influence the proportions of the requirements obtained from the "day" and "night" paddocks.

Generally the leys were strip-grazed using an electric fence when the herbage was 6-10 inches high, and the fields of permanent pasture were grazed extensively when the herbage was 3-6 inches high. It was noticeable that when both a ley and a field of permanent pasture were grazed during alternate "day" and "night" inter-milking periods the number of grazing hours was always higher on the permanent pasture. This was also true in the case of maiden seeds being grazed for the first time when the herbage was short. The number of grazing hours, therefore, appears to be greater when the herbage is short and smaller with long herbage.

With reference to Tables I and II it also appeared that the time spent grazing was greater with wet herbage and smaller with dry herbage.

Allowing for these three factors the information in Table II suggests that when no supplementary feeding was given there was a positive correlation between the number of hours spent grazing and the milk yield. The amount of concentrates fed tended to mask the cor-

TABLE 1.
Summary of 10 Studies, 1949-1950—Grazing and Cudding, etc., within 24 hours.

Study No.	Name of Cow	Date	Grazing		Chewing Cud		Condition of Herbage	Length of Herbage	Drinking water	Temperature Range (°F)	Concs. Fed (lb.)	Defecations	Milk Yields (lb.)
			"Day" "Night"	Total	"Day" "Night"	Total							
			%	hr. mn.	(%)	hr. mn.							
1	Buttercup	1949 6th-7th May	36.5	7 15	27.3	72.7	6 3	mainly wet	Medium	1	44-64	13	30½
2	Buttercup	10-11 June	32.9	7 5	23.3	76.7	5 57	dry	Medium to long	2	53-74	4 13	29
3	Snowdrop	1-2 July	44.8	5 39	50.9	49.2	9 12	dry	medium	2	52-98	5½ 18	27½
4	Buttercup	28-29 July	33.9	7 49	28.9	71.1	5 45	dry	short	3	53-76	4½ 12	23
5	Marvel	31 Aug.-1 Sept.	29.9	7 48	22.7	77.3	6 1	wet	short	3	57-76	11 26	52½
Average Figures			36.5	7 7	27.8	72.2							
6	Buttercup	1950 21-22 April	49.7	6 36	21.7	78.3	6 51	relatively dry	medium to long	2	38-63	6½ 16	31½
7	Winsome Lass	26-27 May	34.8	6 13	29.2	70.8	6 25	dry	short to medium	3	43-62	10 18	48½
8	Buttercup	23-24 June	47.4	6 26	11.2	88.8	4 18	relatively dry	short to medium	2	45-70	2 13	27
9	Winsome Lass	20-21 July	49.5	7 28	22.9	77.1	5 44	dry & wet	medium to long	2	55-81	2 18	25½
10	Buttercup	23-24 Aug.	60.7	7 20	18.9	81.1	6 42	wet	short and long	2	52-65	- 14	13½
Average Figures			48.8	6 48	23.9	76.1							
Overall Averages			42.0	6 58	25.7	74.3	6 18		2.2		4½	16	30½

TABLE II.
 "BUTTERCUP"—Summary of 6 Studies on One Cow, 1949-1950—Grazing and Cudding, etc., within 24 hours.

Study No.	Date	Grazing.			Chewing Cud		Condition of Herbage	Length of Herbage	Drinking Water	Temperature range (°F)	Concs. fed (lb.)	Defecations	Milk Yield (lb.)
		"Day"	"Night"	Total	"Day"	"Night"							
		(%)	(%)	hr. mn.	(%)	(%)							
1	1949 6-7 May	36.5	63.5	7 15	27.3	72.7	6 3	mainly wet	1	44-64	-	13	30½
2	10-11 June	32.9	67.1	7 5	23.3	76.7	5 57	dry	2	53-74	4	13	29
4	28-29 July	33.9	66.1	7 49	28.9	71.1	5 45	dry	3	53-76	4½	12	23
Average figures		39.7	60.3	7 23	26.5	73.5	5 55		2		3	13	27½
1950													
6	21-22 April	49.7	50.3	6 36	21.7	78.3	6 51	relatively dry	2	38-63	6½	16	31½
8	23-24 June	47.4	52.6	6 26	11.2	88.8	4 18	relatively dry	2	45-70	2	13	27
10	23-24 Aug.	60.7	39.3	7 20	18.9	81.1	6 42	wet	2	52-65	-	14	13½
Average figures		52.8	47.2	6 47	17.3	82.7	5 57		2		3	14	24
Overall Averages		45.9	54.1	7 5	21.9	78.1	5 56		2		3	13-14	25½

Periodicity of Grazing Cycles.

Note :—The times stated refer to British Summer Time.

Note :—The times stated refer to British Summer Time.

TABLE IV.

Distribution of Grazing Hours between Periods of Daylight and Darkness.

Study No.	Date	Daylight		Darkness	
		Time	Percentage	Time	Percentage
	1949				
1	6th-7th May	6 hrs. 7 mins.	84.4%	1 hr. 8 mins.	15.6%
2	10th-11th June	7 hrs. 5 mins.	100%		
3	1st-2nd July	5 hrs. 39 mins.	100%		
4	28th-29th July	7 hrs. 49 min.	100%		
5	31st Aug.-1st Sept.	5 hrs. 32 mins.	70.9%	2 hrs. 16 mins.	29.1%
	1950				
6	21st-22nd April	5 hrs. 30 mins.	83.3%	1 hr. 6 mins.	16.7%
7	26th-27th May	5 hrs. 45 mins.	92.5%	28 mins.	7.5%
8	23rd-24th June	6 hrs. 26 mins.	100%		
9	20th-21st July	7 hrs. 28 mins.	100%		
10	23rd-24th August	6 hrs. 54 mins.	94.1%	26 mins.	5.9%
	Aver. Figures	6 hrs. 25 mins.	92.3%	32 mins.	7.7%

TABLE V.

Distribution of Number of Defecations and Urinations.

Study No.	"Day" Paddock		"Night" Paddock		Yards & Milking Parlour		Total	
	Defecations	Urinations	Defecations	Urinations	Defecations	Urinations	Defecations	Urinations
1	3	2	7	6	3	4	13	12
2	4	3	7	5	2	1	13	9
3	4	2	12	6	2	2	18	10
4	2	4	9	4	1	1	12	9
5	5	3	17	10	4	2	26	15
6	3	2	4	5	9	2	16	9
7	3	2	7	4	8	5	18	1
8	4	3	6	8	3	2	13	13
9	6	6	8	6	4	6	18	18
10	4	6	7	6	3	3	14	15
Mean	3.8	3.3	8.4	6.0	3.9	2.8	16.1	12.1
%	23.6	27.5	52.2	50.0	24.2	23.5	100	100

relation and the times spent chewing cud may be proportionately greater.

While it was not possible to weigh the excreta the figures in Table II suggest that the number of defecations increased with milk production, and therefore grass consumption.

The figures for chewing cud may serve to illustrate the nature of the herbage consumed. For example in Study No. 3, the herd was allowed access to two fields, one a Cocksfoot ley which was strip-grazed and the other a field of permanent pasture which had been topped with the mower the previous day. The toppings had not been removed from the field and were in the condition of a light hay crop. This study was conducted during the 1949 drought when the herbage was very dry and the time spent chewing cud was high, 9 hours 12 minutes. In Study No. 8 the "day" paddock was a field of maiden seeds being grazed for the first time. The grass was about three inches high, very lush, with a low fibre content, and the time required for chewing cud was only 4 hours 18 minutes. The time required appeared to be correlated with a low moisture content and a high proportion of fibre.

The information collected from the 10 studies showed that the cows drank water on one, two or three occasions during 24 hours. Generally, drinking took place some time between the afternoon milking and the beginning of the night darkness, but where the cow drank on three occasions it often drank either immediately before or immediately after the morning milking or sometime around mid-day. Drinking usually took place between grazing cycles.

Table III shows that on average the cows had five grazing cycles during 24 hours, while Table IV gives the periods of grazing split between periods of light and darkness. The average figures indicate that only 7.7% of the grazing time took place during the hours of darkness. It would appear that grazing was independent of change of light. The figures suggest that it became necessary for the cow to graze during darkness only, when the hours of daylight were limited, i.e., in spring and autumn.

The behaviour of the grazing animal throughout the five grazing cycles was very similar. At the beginning when the cow had an appetite for food it was not so particular in selecting

leafy herbage and ate grass stems in the hay stage as well as leafy pasture; also, there was a higher incidence of intermittent grazing at the beginning of each grazing cycle. Soon the cows settled down to continuous grazing and later, as their appetite diminished, they became more selective so that, for example, grass in the hay stage was avoided. Towards the end of the cycle leafy herbage only, was eaten and grazing again tended to become intermittent rather than continuous.

It was interesting to note that the cow under observation often ate the tips of the leaves of the grasses before starting on the remainder of the grass shoots, and this was generally true of the rest of the herd. Under conditions of extensive grazing when the dairy herd was given access to fresh pasture the cows wandered all round the field eating off the tips of the leaves. When strip-grazing they would eat off all the tips on the "fresh" strip and later eat the shoots down to ground level. Since the tips of the leaves are richer in protein than the remainder of the grass plants, the evidence indicates that strip grazing provides a better balanced daily ration of grass nutrients than does extensive or rotational grazing.

In one field which was strip-grazed for "early bite" in the spring of 1950 a hay crop was taken in June, followed by a cut for silage in late July. The ley was again strip-grazed in the fourth week of August, during which the trial was conducted, and by that time all the droppings from the first grazing were well rotted and had lost their taint. The strip was eaten well down, thereby giving ample proof that the difficulty of increased soiling of the pasture by dung and urine, resulting from the heavier rate of stocking which is practised with strip-grazing, was overcome by taking cuts between the grazings.

On a large number of dairy farms by the use of a "night" paddock the dairy herd is allowed to graze a particular field during the daytime and is turned into a field near the buildings at night. Under these conditions it is possible that there may be a transference of fertility from the "day" to the "night" paddock. Table V shows the number of defecations and urinations which occurred while the cows were at pasture during both inter-milking periods, and in the yards and milking parlour during both milkings.

While the table shows the actual number of

droppings, the figures bear no relation to quantity. Nevertheless, the average figures indicate that almost twice as much dung and urine was dropped on the "night" paddock as compared with the "day" paddock, and therefore a transference of fertility occurred.

An important feature was the total loss of dung and urine when the cows were off pasture during milking hours. When the percentage figures in Table V for the proportions of dung and urine dropped on the "day" and "night" paddocks are deducted from the total, the average losses are 24.2% of dung and 23.5% of urine. These losses appear to be high, but with suitable buildings and storage facilities, much of the dung and urine dropped on the yards and in the milking parlour, can be conserved for use on the land at a later date.

Summary

The behaviour of grazing dairy cows was studied under commercial conditions in a series of ten observations covering two grazing seasons. In all cases one Ayrshire cow in milk was under observation for a period of 24 hours commencing at 2.30 p.m. and the times of milking were 6.00 a.m. and 3.00 p.m.

- (1) The average time spent grazing was 7 hours and approximately $6\frac{1}{4}$ hours were spent chewing cud.
- (2) The average figures indicated that 42% of the grazing time took place during the "day" inter-milking period and 58% during the "night" period.
- (3) The grazing time appeared to be correlated

with the length and dampness of the herbage and the milk yield.

- (4) The time spent chewing cud appeared to be correlated with a low moisture content and a high proportion of fibre in the herbage consumed.
- (5) In warm weather the cows preferred to graze during the cooler periods in the morning and evening, and to rest during period of high temperatures.
- (6) The cows drank water on one, two or three occasions during 24 hours.
- (7) The cows had five grazing cycles during 24 hours and the time between cycles was occupied by chewing cud and resting.
- (8) Grazing was independent of change of light and some grazing took place during the hours of darkness, particularly in spring and autumn.
- (9) The cows first ate the tips of grass leaves before starting on the remainder of the shoots.
- (10) When dual grazing is practised there is likely to be a transference of fertility from the "day" to the "night" paddock.

Acknowledgements

Grateful thanks are due to my colleagues for their interest in this work, in particular Mr. W. S. Ferguson for his helpful suggestions and encouragement, and to Imperial Chemical Industries Limited for granting me permission to publish this paper.

Responses of Wild Rats to Offensive Smells and Tastes

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Confident assertions are commonly made about the attractiveness or deterrent action to the common brown rat (*Rattus norvegicus* Berkenhout) of various olfactory and gustatory stimuli, but little scientific work on the subject has been published. The present report describes a method of studying the responses of rats to these stimuli, and the results of some preliminary experiments (see Table 1). The results are published now, since facilities for this work are no longer available.

Method

The observations were made on enclosed colonies of wild rats maintained in proofed rooms of floor area of about 180 sq. ft. The number of rats varied from 5 to 30. Each colony had a nesting site of tins and sacking which was left undisturbed. The main food was whole wheat, but the rats received also about 1,000 g. cabbage once a week and 500 g. liver once a fortnight. There was a constant supply of fresh water. A general description of the behaviour of these rats is given elsewhere (Barnett & Spencer, 1951).

The wheat was supplied on two specially designed bait boxes. Each box was one foot square in plan, made of wood with a lid of perforated zinc. The two boxes were put about two feet apart and about seven feet from the nest. To test response to odours, a pad of cotton wool was sprinkled with 2-3 g. of the substance to be tested and put in an open tin inside one of the boxes. A similar tin with untreated cotton wool was put in the second box. A freshly sprinkled pad was prepared daily. Except where otherwise mentioned below, the boxes were daily alternated in position, so that one box always contained the substance under test but its position was changed each day. The substances were aniseed oil, butyric acid, peppermint oil and n-butyl mercaptan.

In four additional experiments, the substance tested was mixed with the wheat. In one (3/2) the aniseed oil was mixed with the wheat in

the proportion of 2.5 g. of oil to 100 g. of wheat. This was just enough to coat each grain with oil. In other experiments (1/4 and 7/4) arachis oil was mixed with both lots of wheat, but aniseed was added to one lot in the proportion of one drop to 100 ml. of arachis oil. In one experiment (7/13) the same procedure was adopted, but with a drop of butyric acid instead of aniseed. In all three of these experiments the proportion of arachis oil to wheat, with or without the substance under test, was 2.5 g. arachis to 100 g. wheat, and the mixtures were offered in alternate compartments of a bait tray with six segments (Barnett & Spencer, 1952).

Results

(a) Aniseed.

No clear differential response could be detected when aniseed was put inside the boxes. The authors could detect the aniseed at 2-3 inches from the lid, but the rats showed no response, even at the beginning of feeding. In experiment 3/1 (fig. 1) slightly less wheat was

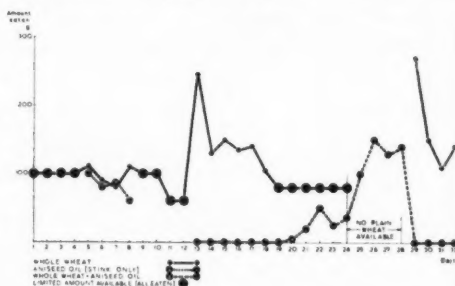


Fig. 1. Effect of aniseed odour and taste.

taken from the box containing aniseed, but the difference was too small to be significant. In experiment 2/2 (fig. 2) for the first 8 days the rats showed a marked preference for the wheat on the box which did not contain aniseed. The aniseed was then put in this preferred box, and after the change a slight preference was

TABLE I

Test	Character of test	Mean daily take Calories	No. of rats	Day temp. range °F	Range relative humidity %	Date 1949	Result
3/1	Aniseed odour	570 (3 days)	5	40-48	68-86	12-15/3	Inconclusive
2/2	Aniseed odour	1,031	16	62-81	68-95	3-16/9	Inconclusive
3/2	Aniseed taste	447 (5 days)	5	42-52	63-87	20-25/3	Wheat-aniseed mixture avoided
1/4	Aniseed taste : wheat+arachis oil wheat+arachis+aniseed	545 332	-	62-81	68-90	3-13/9	Less aniseed mixture taken
7/4	Aniseed taste : wheat+arachis oil wheat+arachis+aniseed	1,021 638	-	60-67	70-89	16-28/9	Less aniseed mixture taken
3/3	n-butyl mercaptan odour	641	10	55-60	58-82	29/5-3/6	Odour avoided
6/8	n-butyric acid odour	853	14	41-45	77-92	16-21/12	Inconclusive
7/13	n-butyric acid taste : wheat+arachis oil wheat+arachis+butyric acid	1,936 867	37	41-50	83-93	20-26/12	Less butyric acid mixture taken
6/9	Peppermint oil odour	1,316	14	44-50	85-93	22-27/12	After three days, odour avoided

shown, not for one particular box, but for one particular place, regardless of which box was there, or whether aniseed was present or not.

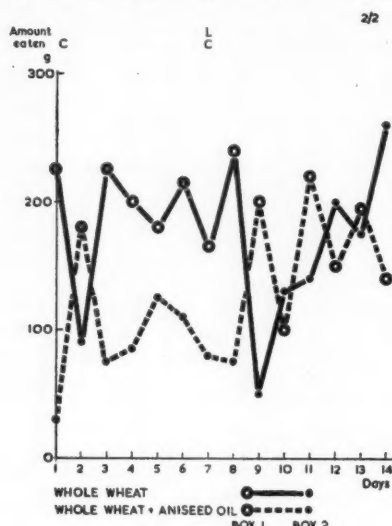


Fig. 2. Effect of aniseed odour.

When aniseed was mixed with the wheat (experiment 3/2) there was an immediate response (fig. 1). Provided that there was a surplus of plain wheat present none of the wheat mixed with aniseed was taken. By reducing the supply of plain wheat it was possible to induce the rats to eat the mixture, but as soon as a surplus of plain wheat was restored the mixture was left untouched. The high take when plain wheat was restored suggests that there was under-consumption of the aniseed when only the mixture was available.

During experiment 3/2 the behaviour of the rats was watched, for part of the time, through an observation window. When the aniseed mixture and plain wheat were both present the rats rejected the former without tasting it. They sniffed at it, sometimes several times, but were never observed to take contaminated grains into their mouths. When hunger drove the rats to eating the aniseed mixture, the pile of wheat was much more disturbed than usual, and more residual fragments of grains were left. In two other experiments (1/4 and 7/4), the amount of aniseed present was greatly reduced, and both bait mixtures contained arachis oil (figs 3 and 4). In both experiments

the gross take of the mixture containing aniseed was less than that of the other. On only one day, in one experiment, was more of the aniseed mixture taken, and this was the first day of experiment 1/4; the daily variation

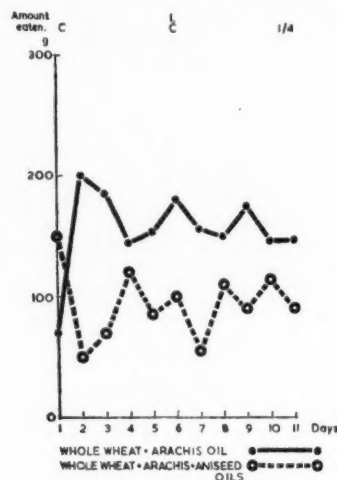


Fig. 3. Effect of aniseed taste.

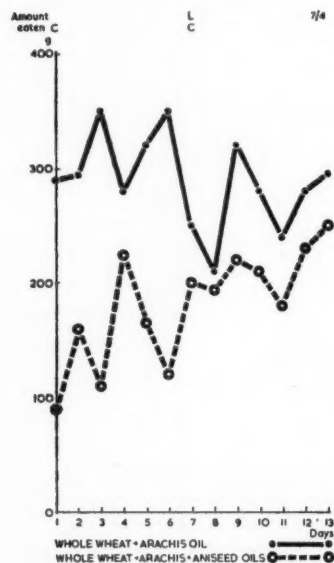


Fig. 4. Effect of aniseed taste.

in the amount taken reflects a tendency, observed

also in previous experiments on this colony, to prefer one of the two positions in which the boxes were placed (cf. Barnett & Spencer, 1952).

(b) *n*-butyl mercaptan.

The odour of mercaptan had a marked deterrent effect. After the first night, when the rats were hungry, only relatively small amounts of wheat were taken from the box containing mercaptan; the wheat was only slightly disturbed, as though rats had snatched a few mouthfuls from the top of the pile. The wheat from the other box was scattered, as usually happens when rats feed at the box itself.

As in the other experiments the boxes themselves were interchanged in position for the first four nights. For the fifth night the mercaptan box was washed and dried; (this procedure did not entirely dispel the odour). The mercaptan was then placed in the box which had hitherto not contained it. On this night, the fifth, there was a rather higher take from the mercaptan box. The following night the boxes themselves were again interchanged, and the take from the mercaptan box fell (fig. 5).

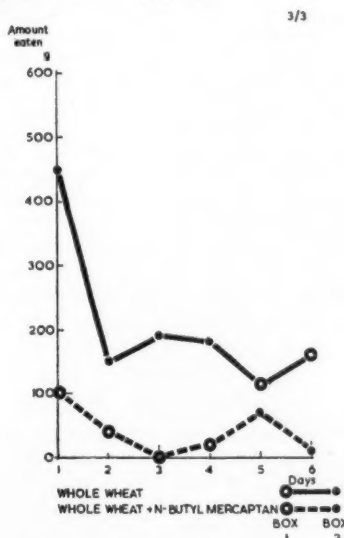


Fig. 5. Effect of mercaptan odour.

(c) *Butyric acid*.

No response to butyric acid could be detected when it was inside one of the boxes (experiment 6/8, fig. 6). In this experiment the rats developed a marked place preference after the first

two days, and took most of the wheat from one box regardless of whether the odour was present or not.

In experiment 7/13 the butyric acid was present with arachis oil, in the wheat; faced with this choice the rats consistently preferred

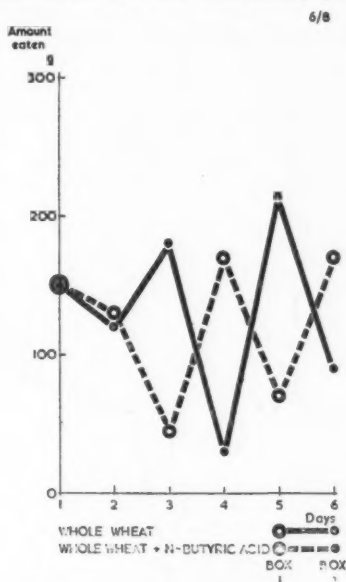


Fig. 6. Effect of butyric acid odour.

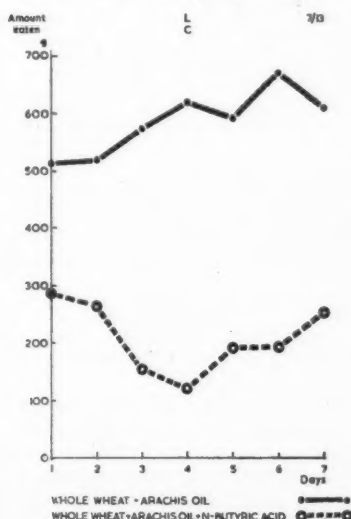


Fig. 7. Effect of butyric acid taste.

the mixture without butyric acid (fig. 7). There was, however, no progressive falling off in the consumption of the butyric acid mixture, and after a decline in the amount taken for the first four days, it rose again for the last three days.

(d) *Peppermint oil.*

One experiment (6/9) was done with peppermint oil placed in one of the two boxes. After three days the rats began to show a preference for the box without the peppermint. At the same time the amount of wheat taken nearly doubled (fig. 8). This extra wheat was after-

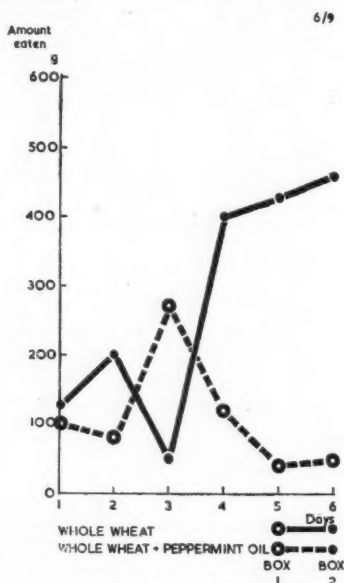


Fig. 8. Effect of peppermint odour.

wards found hoarded in the nesting site. Unfortunately, for administrative reasons, the experiment had to be stopped after six days.

Discussion

The experiments described here are too few for any general conclusions. Four comments may be made.

First, it is shown that aniseed, so long and so widely recommended as an attractant, is in fact a deterrent to wild rats. Direct observation shows that the deterrent effect operates through the olfactory sense when the aniseed is present in considerable quantity in the food itself.

We have not directly observed the behaviour of rats faced with a mixture containing aniseed in very small concentration, although we have shown that such a mixture is avoided.

Second, it is of interest that Scott & Quint (1946) have shown that albino rats do not avoid aniseed or butyric acid as do wild-type *R. norvegicus*. This tends to confirm Keeler's (1942) hypothesis of an association between albinism and a poor olfactory sense.

Third, the results suggest that the presence of an odorous substance not actually mixed with the food becomes important only if the odour is very marked. It is a striking fact that, although, to the human nose, the odour of the mercaptan during experiment 3/3 filled the room and indeed the whole building, the box which contained the mercaptan was avoided by the rats and a normal amount of wheat was taken from the box only two feet away.

A fourth point may be made about the character of the avoidance of distasteful substances. Rats are known to avoid new or unfamiliar objects (Chitty & Shorten, 1946; Shorten, unpublished). This "new object reaction" is overcome as a rule within a few hours or days. In the experiments described here the avoidance displayed is of a different character: we are dealing not with new object reaction but apparently with an innate and not easily alterable aversion to certain olfactory and gustatory stimuli. In two experiments (1/4 and 6/9) the aversion grew rather than declined (cf. Bellack & de Witt, 1949). It is a matter for further experiment whether aversions of this kind can be overcome by conditioning. At present we know only that they can be nullified by hunger.

Summary

1. The presence of aniseed oil below a heap of whole wheat does not act as a deterrent to the common rat, but the presence of aniseed mixed with the wheat acts as a marked deterrent. The effect is through the olfactory sense.
2. The presence of *n*-butyl mercaptan or of peppermint oil below wheat has a deterrent action.
3. Butyric acid below wheat has no effect, but mixed with wheat it has a deterrent action.

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Reviews of Books.

Handbook of Psychological Research on the Rat. An Introduction to Animal Psychology. By N. L. MUNN. New York: Houghton Mifflin Co. 1950. Pp. xxvi + 598; 180 illustrations; 15 tables. 7.50 dollars.

Those who employ the rat in psychological and allied research will be familiar with the author's *An Introduction to Animal Psychology*, published in 1933. That work had, in his own words, "outlived its usefulness as a text and as a review of the literature." The combination of the two aspects in the one volume seemed no longer feasible and, "faced with the alternatives of writing a text or of writing a complete survey," Munn chose the latter.

There are few who will be disappointed with the present work, and none who can deny its extreme usefulness. Leonard Carmichael, the editor of the series in which it appears, describes it as a model of scholarship. That is high praise indeed, but does not appear to be an over-statement. The vast amount of subject matter available has been covered in a lucid and methodical fashion, and it is pleasant to be able to verify that British references have been checked in detail. The author's obvious enthusiasm for his subject is reflected in his style as well as in his documentation, and we can but admire the qualities that have enabled him after an interval of nearly 20 years to review his subject again in such a refreshing manner.

The work is divided into ten sections, viz.: (1) introduction; (2) unlearned behaviour; (3) general activity; (4) motives, emotions and hoarding; (5) sensory processes; (6) the role of sensory processes in maze behaviour; (7) the learning process; (8) some aspects and conditions of learning; (9) systematic psychology; and (10) abnormal and social behaviour. The extensive list of contents, the use of sub-titles and the method of presentation render it a simple matter to look up any particular point.

Every work must have its flaws, and this is no exception, but to discuss minor points or errors would be trivial. The author and those who have helped him to make this significant contribution to psychological literature are to be congratulated. As Leonard Carmichael states, "... the preparation and publication of this book is likely to be recognised in the years ahead as an event of great importance in the history of the exact study of psychology in the science of behaviour."

The Study of Instinct. By N. TINBERGEN. Oxford University Press. 1951. Pp. xii + 228. 25s.

The biologist of to-day would probably claim without fear of contradiction that great progress has been made in our knowledge of the anatomy and physiology of animals and that this knowledge has been most successfully applied; for example in the fields of agriculture and human medicine. Study of the internal structure of animals and of how the components parts function, is much more advanced than is the study of the whole animal and what it does. Ethology or the study of animal behaviour is a comparatively new subject. Readers of Prof. Tinbergen's book however will be impressed by the wealth of material which is now available to the study of ethology and by the amount of critical experimentation which has been carried out in order to analyse causal sequences and determine laws, and by the obvious potential importance of the subject in fields of applied biology.

In the preface the author states that his presentation has a dual aim. First to call attention of Anglo-American workers to research done on the European Continent and published in German, much of which has not penetrated into English and American Science, and secondly to attempt an organisation of ethological problems into a coherent whole.

The first aim is closely related to the second. Perhaps owing to the isolation caused by War and to the fact that the subject matter is of more academic than applied interest, there has been a tendency for ethological problems to be studied along different lines in different countries or within the same country in different scientific departments; for example neuro-physiology in England, the conditioned reflex in the U.S.S.R., neuro-muscular co-ordination in England and the U.S.A., the study of learning by maze technique in the U.S.A., Human psychology and psychiatry are also studied in rather highly specialised departments in many countries. The organisation of ethology into a coherent whole must necessarily take cognizance of all branches of the subject, in whatever country or department they may be developing. Prof. Tinbergen's special contribution to this synthesis is to bring to notice the Continental work on the study of innate behaviour, to which he himself has contributed so much. Although

dealing primarily with instinct or innate behaviour patterns, his book covers a much larger field and it is clear that he has in mind this broader synthesis. This is most obvious perhaps in his conception of the hierarchical organisation of the nervous mechanisms underlying instinctive behaviour. That instinctive behaviour patterns can be classified in hierarchical order is certainly evident and this is an important step taken by the author towards an analysis of ethology, but the nervous mechanisms and neural pathways which are involved have still to be identified and brought into line with the findings of the neuro-physiologist.

It is not an adverse criticism to say that Prof. Tinbergen's book treats of much that is speculative, it is rather a tribute to his gift of inspiring interest in a fascinating subject. Although the arrangement of the material in chapter with headings and sub-headings is not always quite clear, and concentration is required if the main argument is to be followed, each section is well written, examples from field observation, or experimentation, are well chosen and the illustrations and diagrams are excellent. The book should prove of great interest to the professional scientist and to the field naturalist.

ARTHUR WALTON.

The Organisation of Behaviour. A Neuro psychological Theory. By D. O. HEBB. London: Chapman & Hall Ltd. 1949. 32s.

Very few books, covering such a wide field of animal and human behaviour have, in recent years, caused so much interest and controversy as this one.

Professor Hebb sets out to produce a "general theory of behaviour that attempts to bridge the gap between neurophysiology and psychology . . ." and while he admits that the task is not easy, one must agree that he has made a brave attempt.

Starting with two main concepts, (1) that of a "cell-assembly" defined as a diffuse structure of neurones which come to act together owing to repeated stimulation, and (2) that of a "phase sequence"—or succession of actions of different cell-assemblies; Hebb attempts to explain phenomena as diverse as those of visual perception, maze learning, motivation, intelligence, and mental illness. The order in which he treats these and many other subjects is, perhaps, as novel as what he has to say. Throughout

his discussion Hebb tries to steer between the extremes of the old "switch-board" theory, and the later forms of "field-theory" of the Gestalt and other writers.

Every branch of the immense tree is treated with extreme care and knowledge. No careful student can agree with Hebb's speculations on every point; but none can fail to be stimulated by them.

G.C.G.

Books Received

The following books have been received, and it is intended to review them in early issues:

W. C. Allee & Karl P. Schmidt, (1951)
Ecological Animal Geography
New York: John Wiley & Sons, Inc.
London: Chapman & Hall Ltd. 75s.

Marston Bates (1951)
The Nature of Natural History
London: Chapman & Hall Ltd. 16s.

Miriam Rothschild & Theresa Clay, (1952)
Fleas, Flukes and Cuckoos
London: Collins (New Naturalist Library).
21s.

Konrad Z. Lorenz (1952)
King Solomon's Ring
London: Methuen & Co. 15s.

R. A. Hinde, (1952).
The Behaviour of the Great Tit (Parus major) and Some Other Related Species.
Supplement II to *Behaviour*.
Leiden: E. J. Brill, 27 guilders: 54s.

J. P. Scott, *et alia* (1950).
Methodology and Techniques for the Study of Animal Societies.
Vol. 51, Art. 6 (pp. 1001-1122) of the *Annals of the New York Academy of Sciences*. 20s.

James Fisher (1952).
The Fulmar.
London: Collins (New Naturalist Library).
35s.

Eric Simms (1952.)
Bird Migrants. Some Aspects and Observations.
London: Cleaver-Hume Press, Ltd. 15s.

ASSOCIATION NOTES

It is hoped that "Letters to the Editor" will form a regular feature of the *British Journal of Animal Behaviour*, and that preliminary communications relating to original work and also critical contributions relevant to the development of the subject will be submitted for publication.

We still receive many requests for the *Bulletin of Animal Behaviour*, of which nine numbers appeared at irregular intervals. There is a considerable demand from libraries for the first four, which have long been out of print, and we shall be only too glad to receive any copies of these that can be spared. There are still stocks of Nos. 5 to 9 inclusive, and these may be purchased on application to the editorial address.

Despite repeated requests from the Hon. Treasurer, certain members had not, up till the time of going to press, altered their Banker's Orders from the old to the new (£1 1s.) rate of annual subscription. It is to be hoped that they will please do so without delay. Changes of address should be notified without delay to the Hon. Secretary of the Association.

A.N.W.

B.A.C.

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FORTHCOMING CONTRIBUTIONS

Papers received for publication in subsequent issues include the following.

Abstracts of papers presented at Symposium on Shore Ecology :

Heredity and Environment in Mammalian Behaviour. D. O. HEBB.

Display and Mating Behaviour of the Black Grouse. E. O. HÖHN.

The Adaptability of the Homecoming Honeybee. C. R. RIBBANDS and NANCY SPEIRS.

Grazing Behaviour in New Zealand. J. L. CORBETT.

The Grazing Behaviour of Bullocks under Two Methods of Management. J. C. TAYLER.

Grazing Behaviour in Relation to Pasture Management. D. B. JOHNSTONE-WALLACE.

Observations on Grazing Dairy Cows at Henley Manor Farm, Somerset. J. C. WARDROP.

The Grazing Behaviour of Dairy Cattle at the National Institute for Research in Dairying.
M. CASTLE.

The Grazing Behaviour of South Devon Cows. R. J. HALLEY.

Notes on the Behaviour of Desert Locusts in a Light Beam. R. C. RAMSEY and
C. ASHALL.

Hill Sheep and Trace Element Feeding. JAMES STEWART.

The Posture of the Falling Mouse. MR. A. CHANCE.

Grazing Behaviour and Helminthic Disease. E. L. TAYLOR.

Flocks and Herds at Free Range. SIR R. GEORGE STAPLEDON.

Association for the Study of Animal Behaviour

FOUNDED 13TH MARCH, 1936

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- Association's Bankers :* LLOYD'S BANK, LTD., 125, *Oxford Street, London, W. 1*

OBJECTS.

The Association for the Study of Animal Behaviour is a scientific society, founded in 1936. Its aim is to promote and co-ordinate work in animal behaviour, the study of which is of interest or importance to a wide range of biologists, e.g., those engaged in psychology, physiology, zoology, animal husbandry and veterinary science.

Scientific meetings are held, often in conjunction with other societies, and the Association possesses a library from which members may borrow, and to which all members are asked to contribute copies of their publications. From 1936 to 1952 the Association published at irregular intervals the BULLETIN OF ANIMAL BEHAVIOUR. This has now been replaced by a regular quarterly publication, the BRITISH JOURNAL OF ANIMAL BEHAVIOUR, which contains original scientific papers and reviews.

MEMBERSHIP.

Membership is open to all who have a genuine interest in animal behaviour and whose election is approved by Council and confirmed by a general meeting. The annual subscription is £1 1s. and whenever possible should be paid by Banker's Order. Forms of Application for membership may be obtained from the Honorary Secretary.

THE BRITISH JOURNAL OF ANIMAL BEHAVIOUR is published quarterly. Annual subscription, 27s. 6d. U.S.A. and Canada, \$5.00.

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